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Dispersal in the Ordovician: Speciation patterns and paleobiogeographic analyses of brachiopods and trilobites

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ABSTRACT

The Middle to Late Ordovician was a time of profound biotic diversification, paleoecological change, and major climate shifts. Yet studies examining speciation mechanisms and drivers of dispersal are lacking. In this study, we use Bayesian phylogenetics and maximum likelihood analyses in the R package BioGeoBEARS to reanalyze ten published data matrices of brachiopods and trilobites and produce time-calibrated species-level phylogenetic hypotheses with estimated biogeographic histories. Recovered speciation and biogeographic patterns were examined within four time slices to test for changes in speciation type across major tectonic and paleoclimatic events. Statistical model comparison showed that biogeographic models that incorporate long-distance founder-event speciation best fit the data for most clades, which indicates that this speciation type, along with vicariance and traditional dispersal, were important for Paleozoic benthic invertebrates. Speciation by dispersal was common throughout the study interval, but notably elevated during times of climate change. Vicariance events occurred synchronously among brachiopod and trilobite lineages, indicating that tectonic, climate, and ocean processes affected benthic and planktotrophic larvae similarly. Middle Ordovician inter-oceanic dispersal in trilobite lineages was influenced by surface currents along with volcanic island arcs acting as "stepping stones" between areas, indicating most trilobite species may have had a planktic protaspid stage. These factors also influenced brachiopod dispersal across oceanic basins among Laurentia, Avalonia, and Baltica. These results indicate that gyre spin-up and intensification of surface currents were important dispersal mechanisms during this time. Within Laurentia, surface currents, hurricane tracks, and upwelling zones controlled dispersal among basins. Increased speciation during the Middle Ordovician provides support for climatic facilitators for diversification during the Great Ordovician Biodiversification Event. Similarly, increased speciation in Laurentian brachiopod lineages during the Hirnantian indicates that some taxa experienced speciation in relation to major climate changes. Overall, this study demonstrates the substantial power and potential for likelihood-based methods for elucidating biotic patterns during the history of life.

1. Introduction

The Middle to Late Ordovician (~470 to 444 Ma) was a time of profound diversification and paleoecological change. This interval began with the Great Ordovician Biodiversification Event (GOBE), the greatest increase in marine families and genera in the Phanerozoic (Harper, 2006). Associated with this dramatic biodiversity increase, marine ecosystems became considerably more complex, and widespread metazoan reefs appeared for the first time (Sheehan, 1996; Servais et al., 2010). Contrastingly, the Ordovician ended with the Late Ordovician (Hirnantian) Mass Extinction, the second largest of Earth's mass extinctions in terms of taxonomic loss (Bambach et al., 2004). These biotic changes were coincident with and ultimately driven by a series of changes within the Earth system such as shifting oceanographic conditions and climate regimes, increased volcanic activity, and widespread carbonate platforms (Algeo and Seslavinsky, 1995; Miller and Mao, 1995; Young et al., 2010; Pohl et al., 2016a; Rasmussen et al., 2016; Young A.L. et al., 2016; Young S.A. et al., 2016). Biogeographic processes have long been considered critical for facilitating both biodiversity accumulation and ecosystem changes during the Middle to Late Ordovician interval (e.g. Miller, 1997; Harper et al., 2013; Wright and Stigall, 2013a; Trubovitz and Stigall, 2016; Stigall et al., 2017). However, empirical analyses of dispersal pressures and pathways constrained by evolutionary data have been limited to date.

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In this study, we utilize a suite of cutting-edge techniques to estimate biogeographic histories and analyze dispersal processes within the Middle to Late Ordovician shallow marine faunas of Laurentia, with additional data obtained from Baltica, Avalonia, Gondwana, and the intervening Iapetus Ocean. To reconstruct the pattern of dispersal events for the region, species-level phylogenetic hypotheses of rhynchonelliformean brachiopod and trilobite clades were employed in a time-stratigraphic framework across four temporal intervals during the Middle to Late Ordovician, each characterized by a different combination of tectonic and paleoclimatic conditions.

Tremendous methodological developments over the past few decades have provided rigorous analytical tools for examining evolutionary changes within a biogeographic context. Specifically, phylogenetic paleobiogeography has been used to interpret vicariance patterns and dispersal pathways, discern changes in area relationships, and identify areas of origination for both fossil and extant invasive taxa (e.g., Lieberman and Eldredge, 1996; Lieberman, 2003; Folinsbee and Brooks, 2007; Wright and Stigall, 2013a; Bauer and Stigall, 2014). Traditionally, most phylogenetically-informed biogeographic analyses have utilized parsimony-based approaches (e.g., Ladiges et al., 1987; Stigall, 2010; Wojcicki and Brooks, 2005; Escalante et al., 2007). Such approaches have produced novel and insightful results, but typically require assumptions of parsimony and congruence of biogeographic patterns among clades, which may not be valid in all circumstances. Recent developments have expanded the accessibility of maximum likelihood and Bayesian modeling approaches in phylogenetic biogeography (e.g., Sanmartin et al., 2001; Costa, 2010; Litsios et al., 2014; Sorenson et al., 2014; Wood et al., 2014). These methods provide a more robust exploration of probabilistic processes and idiosyncratic patterns. The full suite of phylogenetic biogeographic methods can be utilized with extant taxa; however, the requirement of contemporaneous terminal taxa curtailed the applicability of model-based methods (e.g., LAGRANGE, Ree and Smith, 2008) with fossil data. A newer method, BioGeoBEARS (Matzke, 2013; R Core Team, 2016), removes that limitation, and is thus fully compatible with extinct taxa.

This study is the first to use the maximum likelihood models implemented within the R package BioGeoBEARS to examine evolutionary biogeographic patterns among Paleozoic taxa. Specifically, ten published species-level data matrices of Middle through Late Ordovician rhynchonelliformean brachiopods and trilobites are re-analyzed using Bayesian methods to develop time-calibrated fossil phylogenies ("tip-dating"; Matzke and Wright, 2016; Bapst et al., 2016). These phylogenies are then used in BioGeoBEARS analyses to estimate biogeographic history. The results are interpreted in a paleogeographic and paleoceanographic context through the Middle and Late Ordovician epochs to 1) reconstruct dispersal pathways and identify speciation mode through time, 2) compare shifting biogeographic patterns with paleoceanographic and tectonic reconstructions for the Middle to Late Ordovician, and 3) identify the impact of different environmental factors on biodiversity during the study interval.

1.1. Middle - Late Ordovician biogeography, tectonics, and paleoceanography

1.1.1. Geologic context

Tectonic and paleoceanographic conditions of Laurentia, Baltica, Avalonia, and Gondwana influenced biogeographic patterns of Paleozoic brachiopods and trilobites throughout the Middle to Late Ordovician. The entire study interval was associated with active tectonism and high rates of seafloor spreading (Servais et al., 2010), leading to widely dispersed continents and terranes surrounded by active volcanic island arcs that deposited massive K-bentonite beds in North America, Europe, South America, and China (Cocks and Torsvik, 2002; Huff et al., 1992, 2010; Rasmussen and Harper, 2011). The constriction of the Iapetus Ocean between Laurentia and Baltica and the Tornquist Ocean between Avalonia and Baltica produced volcanic island arcs and led to the eventual collision of these paleocontinents in the latest Ordovician through middle Silurian (Cocks and Torsvik, 2011).

Global climate transitioned from greenhouse to icehouse conditions during the study interval. The Cambrian through Early Ordovician was characterized by very warm global temperatures and high sea-level (Trotter et al., 2008). The Middle Ordovician was an interval of cooling, and continental glaciation may have occurred as early as the Darriwilian Age as hypothesized by high-resolution geochemical, paleoecological, and backstripping studies (Vandenbroucke et al., 2009; Dabard et al., 2015; Amberg et al., 2016; Pohl et al., 2016a; Rasmussen et al., 2016), with some studies indicating glaciation may have taken place as early as the Early Ordovician (e.g., Turner et al., 2011). Continental

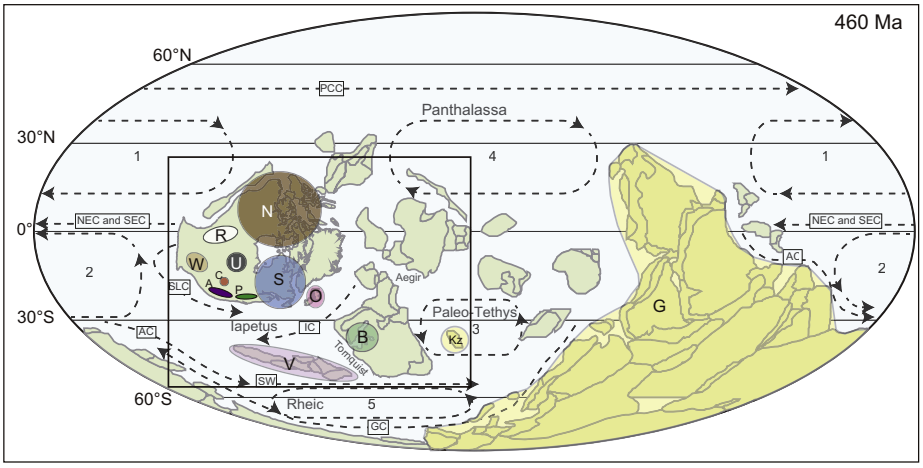

Fig. 1. Paleogeographic reconstruction of the latest Middle Ordovician Darriwilian Age with oceanic basins and major ocean gyres (numbered) and currents (dotted lines). Geographic areas considered in this study are lettered: N, Northern Laurentia (Northwest Territories, Nunavut, British Columbia); R, North of the Transcontinental Arch; W, Western Midcontinent; U, Upper Mississippi Valley; C, Cincinnati basin; A, Southern Appalachian basin; P, Northern Appalachian basin; S, Southern Laurentia (Newfoundland, Quebec, Anticosti Island); O, Scoto-Appalachia; V, Avalonia; B, Baltica; G, Gondwana (Kazakh terranes (Kz), Australia, Japan, Arabia, Turkey, Bohemia, Spain, France). Ocean gyres are as follows: 1, North Panthalassic convergence; 2, South Panthalassic convergence; 3, South Paleo-Tethys convergence; 4, North Paleo-Tethys convergence; and 5, the Rheic convergence. Black boxes denote the names of major ocean currents: PCC, Panthalassic Circumpolar Current; IC, Iapetus Current; SLC, Southern Laurentia Current; NEC and SEC, North and South Equatorial Currents; AC, Antarctic Current; SW, South Westerlies; and GC, Gondwana Current. Large black box around Laurentia, Avalonia, and Baltica denotes the area represented in Fig. 5. Map modified from Torsvik and Cocks (2013); ocean currents and gyres from Pohl et al. (2016b). The paleogeographic maps of the Late Ordovician Sandbian Age from Torsvik and Cocks (2013) are used throughout the text across all four time slices for illustrative purposes, although paleogeography was changing through the study interval.

glaciation was well-developed by the Late Ordovician and likely occurred in pulses separated by relatively stable climate conditions, much like the Milankovitch-controlled glaciations that dominated the late Pliocene and Pleistocene of the Cenozoic (Zachos et al., 2001; Lisiecki, 2010).

Increased tectonic activity during the Middle to Late Ordovician created seafloor spreading centers that initiated rapid northward drift of continents away from Gondwana and produced high first-order sea-level rises, including what may have been the highest sea-levels of the Paleozoic occurring in the Late Ordovician (Hallam, 1992; Haq and Schutter, 2008). Relatedly, epicontinental seas covered large regions of the widely dispersed paleocontinents, which facilitated extensive carbonate sedimentary deposition on tropical shelves (Algeo and Seslavinsky, 1995; Walker et al., 2002).

Ocean surface circulation modeling of the Middle to Late Ordovician oceans by Pohl et al. (2016b) reconstructed five major ocean gyre systems, as previously identified and named by Poussart et al. (1999) and Herrmann et al. (2004), along with several smaller gyres and currents that characterized Ordovician seas (Fig. 1). Notably, these currents could have operated as dispersal vectors among Laurentia, Baltica, and Avalonia, with some influence from Siberia and Gondwana (Pohl et al., 2016b).

1.1.2. Temporal context

The Middle Ordovician Epoch (Dapingian–Darriwilian ages) includes the Great Ordovician Biodiversification Event (GOBE) in which marine invertebrate biodiversity increased dramatically within a 25-million-year timespan (Servais et al., 2010). Recent studies have suggested that increasing homogenization of faunas among paleocontinents began to take place during this time as inter-continental dispersal was facilitated by Baltica moving closer to Laurentia from the southeast and Avalonia shifting to the northeast via the closure of the Tornquist Sea (e.g., Harper et al., 2013; Trubovitz and Stigall, 2016). Contemporaneous with these tectonic constrictions and faunal diversity increases, oceanic cooling on the order of 4–5 °C has been reported for the Baltic basin. This cooling occurred shortly after the Dapingian–Darriwilian boundary and has been interpreted to represent a decline into an icehouse world as continental glaciations began to develop (Rasmussen et al., 2016).

At the start of the Sandbian Age, the Blountian tectophase of the Taconian Orogeny initiated along the southeastern margin of Laurentia (Figs. 2, 3) (Ettensohn, 2010). Accretion of island arcs and microcontinents along this margin led to the formation and subsidence of the Sevier Basin, which stretched from the Alabama to Virginia promontories and incorporated distinct shelf, slope, and basin facies (Shanmugam and Lash, 1982; Ettensohn, 2010). Sedimentation within the epicontinental basins of Laurentia was mainly unaffected, and tropical carbonate deposition prevailed across Laurentia (Holland and Patzkowsky, 1997).

During the late Sandbian Age, the depression of the Sebree Trough initiated over the Precambrian-Early Cambrian Reelfoot Rift (Kolata et al., 2001), nearly synchronous with the initiation of the Taconic tectophase. This narrow depression was located along the eastern edge of the Laurentian midcontinent carbonate platform due to increased tectonic stress (Fig. 2). The Sebree Trough stretched for hundreds of kilometers and funneled cool nutrient-rich waters into the craton from the Iapetus Ocean to the south, resulting in deposition of black shales (Kolata et al., 2001). The influx of oceanic water in addition to the deepening of cratonic basins from the Taconic tectophase may have initiated epicontinental estuarine-like circulation patterns in the midcontinent of Laurentia, generating a density-stratified water column that contained cool, oxygen-poor, phosphate-rich oceanic waters that continued until at least the earliest Katian (Wilde, 1991; Kolata et al., 2001; Young A.L. et al., 2016; Young S.A. et al., 2016; Quinton et al., 2017). Consequently, carbonate platform deposition ceased and a mixed carbonate-clastic facies prevailed within temperate waters across most of east-central Laurentia (Keith, 1989; Ettensohn, 2010). Carbonate deposition resumed during the Katian Age due either to the effective infilling of the Sebree Trough, which reduced upwelling, or to the globally recognized warming trend known as the Boda Event (Fig. 3) (Fortey and Cocks, 2005, but see Cherns and Wheeley, 2007; Kröger et al., 2016).

Significant events of faunal immigration into epicontinental basins occurred during the Late Ordovician. For example, the Katian Richmondian Invasion involved the migration of over 60 extra-basinal genera into the Cincinnati basin from other areas within Laurentia and Baltica (Wright and Stigall, 2013a; Bauer and Stigall, 2014; Lam and Stigall, 2015), which resulted in significant ecosystem restructuring (Patzkowsky and Holland, 1996; Holland, 2008; Stigall, 2010). Even more widespread migration of taxa occurred with the establishment of the Hirnantian fauna during the latest Ordovician.

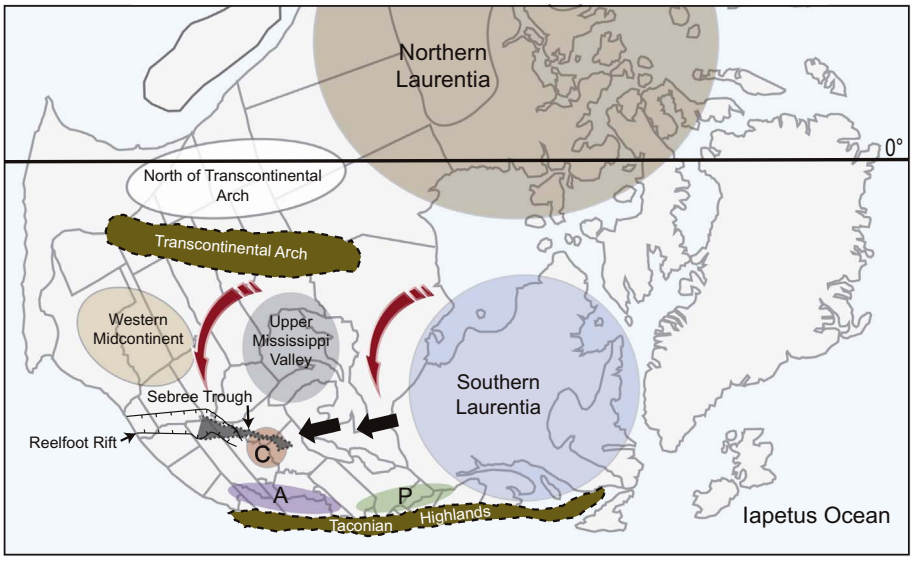

Fig. 2. Paleogeographic map of Laurentia during the late Sandbian showing locations of basins, the Reelfoot Rift that led to the creation of the Sebree Trough, the Transcontinental Arch, and the Taconian Highlands created from the Taconian Orogeny, hurricane tracks (red arrows) and direction of flow of surface currents (black arrows). Basin names and colors correspond to those in Fig. 1. C, Cincinnati basin; A, Southern Appalachian basin; P, Northern Appalachian basin. Paleogeographic map modified after Lam and Stigall (2015) and Kolata et al. (2001). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The Late Ordovician Hirnantian Age includes the end-Ordovician mass extinction event. Mounting evidence indicates that cooling associated with Hirnantian glaciation may have begun in the Middle Ordovician (Saltzman and Young, 2005; Trotter et al., 2008; Rasmussen et al., 2016). Generally, taxonomic loss is thought to have been linked to glacial pulses during the extinction, although Ghienne et al. (2014) suggested a link to the deglaciation intervals. This assumption, however, is not supported by recent modeling scenarios based on rhynchonelliformean brachiopods (Finnegan et al., 2016).

2. Materials and methods

2.1. Temporal and geographic framework

Four time slices, termed T1 through T4, were established to characterize speciation modes across major tectonic and paleoclimatic events (Fig. 3). Because the dominant speciation processes have been previously demonstrated to vary during times of major tectonic and paleoclimatic changes (e.g., Stigall, 2010; Wright and Stigall, 2013a; Stigall et al., 2017), time slice boundaries were defined to coincide with major sedimentological changes within Laurentia, indicative of changing climatic and tectonic conditions. The T1 time slice encompasses the Dapingian and the Darriwilian ages, a time of increased global tectonic activity and major diversification associated with the Great Ordovician Biodiversification Event (Miller and Mao, 1995). The T2 time slice spans the start of the Sandbian Age to the M4/M5 sequence boundary of the Cincinnati basin (late Sandbian) and includes the Blountian tectophase of the Taconian Orogeny (Ettensohn, 1994; Fig. 3). The T3 time slice includes the Taconic tectophase of the Taconian Orogeny. It begins at the M4/M5 sequence boundary of the Cincinnati basin in the late Sandbian Age and ends at the C3/C4 sequence boundary (mid late Katian Age) (Ettensohn, 1994). The T4 time slice includes the time from the C3/C4 sequence boundary to the end of the Hirnantian Age. Although speciation events were reconstructed with high temporal precision, they were grouped into bins of longer duration due to the relatively small number of phylogenies available for analysis and the uneven distribution of biogeographic events within the study interval.

Twelve biogeographic regions were defined for the analysis (Fig. 1). Nine areas were defined within Laurentia based on separation of basins by physical (e.g., the Transcontinental Arch) and thermal barriers (e.g., the deep-water Sebree Trough which was filled with cooler oceanic waters; Fig. 2): Northern Laurentia, North of the Transcontinental Arch, the Western Midcontinent, Upper Mississippi Valley, Cincinnati basin, Southern Appalachian basin, Northern Appalachian basin, Southern Laurentia, and Scoto-Appalachia (Fig. 1). On a global scale, the defined areas follow the Middle to Late Ordovician rhynchonelliform brachiopod provinces of Harper et al. (2013) and the provinces defined by Meidla et al. (2013) for Late Ordovician ostracods. Within Laurentia, the defined areas in this study match those of sponge provinces identified by Carrera and Rigby (1999), as well as the areas of distinctive endemic faunas of conodonts, corals, brachiopods, and ostracod within the continental interior and marginal basins (Amsden, 1974; Thompson and Satterfield, 1975; Elias, 1983; Amsden, 1986; Barrick, 1986; Elias and Young, 1992; Mohibullah et al., 2012). Basins of eastern North America coincide with the aquafacies of Holmden et al. (1998) based on conodont associations for the Late Ordovician of Laurentia. Fewer species occupied the paleocontinents of Avalonia, Baltica, and Gondwana, thus each of these continents were counted as separate geographic areas.

2.2. Species occurrence data

Brachiopod and trilobite taxa were employed as focal taxa for this study because these organisms comprise a substantial and well-sampled component of the Ordovician benthos. This study employs previously published character matrices assembled for species-level phylogenetic analysis (Table 1); even though each incorporated data set examined species as the operational taxonomic unit, some studies encompass a genus and others encompass a whole family. The species-level phylogenetic hypotheses created by parsimony or statistical methods included within this study encompass the majority of species-level phylogenetic hypotheses published for clades during this time interval.

Moreover, brachiopods and trilobites utilized a variety of larval strategies, which permits comparison of dispersal patterns across differing larval phases. Clades used for the analysis were primarily composed of Laurentian and Baltic species to elucidate dispersal patterns within these regions. Members of some clades inhabited basins in Avalonia and Gondwana. Taxa inhabiting these geographically separated areas are incorporated in the analysis because they are valuable for determining large-scale oceanographic patterns. Future analyses would benefit from additional phylogenetic hypotheses of clades other than brachiopods and trilobites not endemic to or originating within Laurentia.

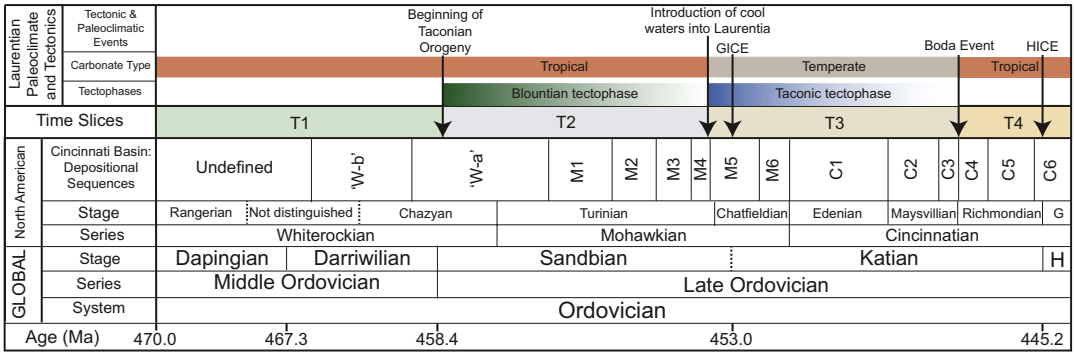

Fig. 3. Chronostratigraphic chart of the Middle to Late Ordovician interval, with global Stages, North American Series, Stages, and 3rd-order depositional sequences of the Cincinnati basin after Bergström et al. (2010) and Holland and Patzkowsky (1996). Ages for the base of each global Stage are from Cooper and Sadler (2012). Time slices used in this study (T1–T4) are indicated above the depositional sequences. Taconian tectophases and dominant carbonate type indicate activity and sedimentation that occurred on the southern margin of Laurentia. Key paleoclimatic events and carbon isotope excursions are also noted. Depositional sequences that begin in the Whiterockian Series of North America are labeled 'W-a' and 'W-b' pending further investigation. Abbreviations: GICE, Guttenberg $\delta^{13}C$ excursion; HICE, Hirnantian $\delta^{13}C$ excursion; G, Gamachian; H, Hirnantian. Taconian tectophases after Ettensohn (2010); occurrence of GICE after Young et al. (2005); occurrence of Boda Event after Fortey and Cocks (2005); occurrence of HICE after Bergström et al. (2006).

Table 1
Focal taxa and their stratigraphic ranges incorporated within the study.

Clade		Clade size	Stratigraphic range	Reference
Eochonetes	Brachiopoda	14	Sandbian-Aeronian	Bauer and Stigall, 2016
Glyptorthis	Brachiopoda	23	Darriwilian-Aeronian	Wright and Stigall, 2013b
Hebertella	Brachiopoda	10	Sandbian-Aeronian	Wright and Stigall, 2014
Plaesiomys	Brachiopoda	10	Katian-Rhuddanian	Wright and Stigall, 2014
Bumastoides	Trilobita	12	Sandbian-Rhuddanian	Carlucci et al., 2012
Deiphoninae	Trilobita	21	Darriwilian-Ludfordian	Congreve and Lieberman, 2010
Flexicalymene	Trilobita	14	Sandbian-Aeronian	Hunda and Hughes, 2007
Homalonotidae	Trilobita	15	Dapingian-Homerian	Congreve and Lieberman, 2008
Tetralichinae	Trilobita	12	Darriwilian-Sandbian	Carlucci et al., 2010
Thaleops	Trilobita	19	Darriwilian-Katian	Amati and Westrop, 2004

Geographic and stratigraphic occurrence data were compiled for each species using published literature and online diversity databases such as iDigBio (www.idigbio.org), the Paleobiology Database (www.paleobiodb.org), and the Digital Atlas of Ordovician Life (www.ordovicianatlas.org; Stigall et al., 2014) (Table 1, Supplemental Table S1). A detailed correlation chart was developed to place each species occurrence within the correct time slice for analysis. Over sixty stratigraphic columns of the geographic area and stratigraphic formations occupied by focal species were correlated across the Middle through Late Ordovician using published literature (Supplemental Table S1, Supplemental Fig. S2). Correlations were based on conodont and graptolite biostratigraphy and chemostratigraphy (e.g., Young et al., 2008; Bergström et al., 2010) (Supplemental Information S3). Correlations for formations and basins within Laurentia and Baltica (e.g., North of the Transcontinental Arch, Upper Mississippi Valley, and the Baltic basin) were adjusted in consultation with Dr. Stig Bergström (pers. comm. 2014). Temporal estimates for each species necessary for the Bayesian analyses were interpolated from bentonite horizon ages published in Cooper and Sadler (2012).

2.3. Phylogenetic framework

The biogeographic analyses require estimates of absolute temporal length of branches on each phylogeny, the biogeographic area(s) occupied by each species, and a fully bifurcating phylogenic topology. Thus, the use of parsimony trees that have been time-scaled through a minimum-age method, while usable for parsimony-based biogeography analyses, are not appropriate for probabilistic, likelihood-based methods such as LAGRANGE and BioGeoBEARS, where some parameters are rates of change per time unit along branches. Therefore, the originally published data matrices for the clades used in this study were reanalyzed using Bayesian tip-dating methods in Beast2 (Bouckaert et al., 2014) with unweighted characters. "BEASTmasteR," a collection of R functions that read in NEXUS character matrices and an Excel file containing dates, priors, and run settings (Matzke, 2016; Matzke, 2017), was used to convert each data matrix into the complex XML format required for Beast2. The use of BEASTmasteR meant that each of the 10 different clade analyses could be set up simply by copying the Excel settings file, pasting in new species names and date information from our dates database, and re-running the BEASTmasteR script. This process is much less error-prone than attempting to manually set up all the necessary dates, priors, and settings 10 times independently in BEAUTi (the Graphical User Interface (GUI) commonly used to set up Beast2 analyses).

Bayesian tip-dating is a rapidly moving field, as the models involved can be complex and parameter-rich. Thus, some published dating studies attempt to maintain maximum agnosticism about the choice of clock models, tree models, and/or priors, and attempt to choose the best model by brute-force computation across many or all possible models. This strategy is inappropriate in the present case, because we had no confidence that the small datasets would support the most complex models or models with more challenging mixing properties. Furthermore, our only goal was to estimate divergence dates that were more realistic than those obtained from a minimum-age parsimony method. Therefore, we privileged simpler/older models that we judged most likely to mix well for small datasets. The same setup was used for each run.

The tree model used was Birth-Death with Serial Sampling (BDSS; Stadler, 2010). Due to the small number of species, a model allowing the possibility of sampled ancestors was not used. The site model was Markov-*k* (Lewis, 2001) with an ascertainment-bias correction for the unobservability of invariant characters (M*k*v, Felsenstein, 1992) in character matrices originally designed for parsimony inference. An M*k*-ParsInf model was not attempted due to the dramatically slower calculation time (Matzke and Irmis, 2017, in press), and might have poor performance for small datasets (Allman et al., 2010). Among-site rate variation was modeled with a discretized gamma distribution with 4 categories. A strict clock (with a flat Uniform (0,10) prior on clock rate) was used for each run. This was chosen because (a) small datasets were unlikely to support good mixing under a relaxed clock analysis, (b) preliminary analysis indicated substantial date uncertainty (due to wide date ranges for some fossil tips) even in a strict clock analysis, and (c) our only goal was to get more realistic average date estimates for each clade, not to exhaustively characterize all possible sources of uncertainty. Each analysis was run for 100 million Markov chain Monte Carlo (MCMC) steps, saving a tree every 50,000 steps. This produced Estimated Sample Sizes (ESSs) above 200 for all parameters in the Tracer plots (the lowest ESS across all 10 analyses was 576, and almost all parameters had ESSs above 1200). TreeAnnotator was used on the last 50% of each run to produce a summary dated tree using Maximum Clade Credibility (MCC). The MCC trees were used for downstream biogeography analysis for each clade.

2.4. Probabilistic biogeographic analyses

Probabilistic inference of ancestral geographic ranges was conducted with the R package BioGeoBEARS (Matzke, 2013; R Core Team, 2016). To date, this method has been primarily applied by Cenozoic and Mesozoic biogeographers to discern dispersal and vicariance patterns within extant vertebrate, insect, and plant clades (e.g., Pyron, 2014; Thacker, 2015; Dantas et al., 2016; Dupin et al., 2016; Fagua et al., 2016; Gorscak and O'Connor, 2016; Klaus et al., 2016; Poropat et al., 2016; Toussaint and Balke, 2016). In BioGeoBEARS, probabilistic biogeographic models are fit to data using Maximum Likelihood (ML). Geography is modeled as presence and absence in a series of discrete areas. The probabilistic models allow geographic range to evolve along phylogenic branches using a dispersal-extinction (meaning range-expansion and range-contraction) process, controlled by the rate parameters *d* and *e*. Ranges can change during cladogenesis under several fixed models that can be modified by a *j* parameter controlling the relative weight of jump dispersal, also known as founder-event speciation. In founder-event speciation, speciation approximately coincides

with a dispersal event; while dispersal-associated speciation appears rapid at a phylogenetic time-scale, this does not necessarily mean literal "instantaneous" speciation, nor does it require assuming the importance of the population-genetic founder effect. After ML optimization of each model, statistical model comparison (Burnham and Anderson, 2002) was used to determine the best-fit models (Matzke, 2013).

As the phylogenies are not ultrametric (they are tip-dated), and this is one of the first all-fossils BioGeoBEARS studies, it is worth commenting briefly on the use of fossils in probabilistic biogeography. BioGeoBEARS is programmed to use the input branch lengths appropriately in likelihood calculations, even if the tree is non-ultrametric and even for time-stratified analyses (wherein changing geography is represented by changing rate multipliers in different time bins; This requires the complex computational operation of tracking which branch segments are in which time bins). Fossil side-branches are treated the same as other branches, except that short branches with lengths < 0.000001 million years are used to represent hypothesized or inferred direct ancestor fossils. Cladogenesis processes would not be used for these nodes on the tree, as they do not represent cladogenesis events. In addition, since fossil specimens might represent presence in a region, but absence of fossils might not represent true absence (depending upon background information about the thoroughness of sampling in the region, etc.), users can code areas as ambiguous (using a "?") if their data is agnostic about the presence of a particular species in a particular region. In the present study, we used the simplest options (none of the tip species are direct ancestors; all fossil ranges are taken to represent true presence/absence data).

Twelve discrete areas used in the BioGeoBEARS analysis (Fig. 1) are defined above from species occurrence data (Supplemental Table S1). Time-calibrated phylogenies from the BEAST2 analyses were converted to Newick files for use in analyses.

Three models from the BioGeoBEARS analyses were compared: Dispersal-extinction-cladogenesis (DEC) (Ree, 2005; Ree and Smith, 2008), DIVALIKE, and BAYAREALIKE. DEC allows single-area sympatry, subset sympatry, and narrow vicariance at cladogenesis. The model assumes that at cladogenesis at least one daughter only occupies a single area (thus, ABCD- > A, BCD is an allowed vicariance event, but ABCD- > AB, CD is not). The second model, DIVALIKE, implements the cladogenetic processes assumed by dispersal-vicariance analysis (DIVA) (Ronquist, 1997) in a likelihood framework, namely single area sympatry and any type of vicariance, but no subset sympatry. Finally, the BAYAREALIKE model implements the cladogenetic processes assumed by the BayArea program (sympatric speciation only, but including widespread sympatry across several areas; Landis et al., 2013). Each of these base models was also modified to produce founder-event speciation "+J" models (DEC + J, DIVALIKE + J, BAYAREALIKE + J), for a total of six models. Founder-event speciation has long been considered a crucial speciation process among island clades (Cowie and Holland, 2006; Templeton, 2008; Gillespie et al., 2012), an interpretation supported by Matzke (2014). The use of these models in this study provides a framework to interpret results of maximum likelihood analyses and to assess whether previously untested founder-event speciation was important for trans-Iapetus dispersal in the Ordovician Period, as previously published biogeographic analyses of this region and time-period used parsimony-based methods that do not have this capability.

BioGeoBEARS analyses were conducted without dispersal constraints, thus directionality and timing of speciation events were uninhibited. The number of areas any taxa could occupy (max_range_size) was set to either 3 or the maximum number of areas occupied by any one species per phylogeny, whichever was larger, in order to limit the size of the state space and avoid very long computation times. Models for each clade were compared using Akaike Information Criterion (AIC), corrected AIC (AICc), the difference between the best model and others (ΔAICc), and the AICc weight (ω_i) as calculated from the log likelihood (lnL) value for each model (Table 2; Burnham and Anderson, 2002). AICc values were calculated using the number of taxa per phylogeny as sample size (O'Meara et al., 2006).

Ancestral range estimation was performed under each model, and the estimates for the best-fitting model for each clade were used to study the biogeography of speciation processes through time. Types of cladogenesis events were counted in each of the four time slices through the Middle to Late Ordovician (Figs. 4, 5). Speciation events occurring at the boundary between two time slices were counted as occurring within the later time interval because that interval was more likely to include documented occurrences for the species.

All scripts and input/output files for the BEAST 2 and BioGeoBEARS analyses are archived on GitHub at https://github.com/nmatzke/Ordovician_dispersal.

3. Results

3.1. Ancestral range estimation and speciation mode analysis

Across the 10 clades, the best-fitting base model varied among DEC and DIVALIKE models. Seven out of ten clades favored "+J" model variants, signifying that founder-event speciation was an important process in Ordovician brachiopod and trilobite clades (Table 2). Within these clades, the "+J" parameter is small relative to the maximum attainable weight (3.0 for DEC + J, 2.0 for DIVALIKE + J), indicating that vicariance and traditional (range-expansion) dispersal were also important processes operating within these clades. It should be noted that clades where most of the tips inhabit single areas will tend to favor "+J" models. Therefore, jump dispersal will tend to be favored if geographic ranges are coded based on specimen location data instead of species ranges based on collective species occurrences. This could lead to erroneous conclusions about the origination and mode of speciation prominent within a clade. However, incomplete occurrence data was not a significant factor in this study, as all geographic ranges were constructed based on several occurrences per species. The clades that did not favor models with the "+J" parameter (*Bumastoides*, *Flexicalymene*, *Plaesiomys*) are endemic to basins within Laurentia.

BioGeoBEARS ancestral area estimates indicated high probability of occurrence for few areas for most nodes in the phylogenies, indicating that ancestral areas were inferred with high confidence (see pie charts at nodes of phylogenies from the BioGeoBEARS analyses in GitHub, https://github.com/nmatzke/Ordovician_dispersal). This suggests clear biogeographic signals in the data.

Of the 140 internal nodes comprising the ten phylogenetic hypotheses analyzed, 106 could be characterized by allopatric speciation via vicariance or dispersal processes (Table 3, Figs. 4, 5). The other 34 nodes were consistent with sympatric speciation within the same biogeographic area(s). Among the 106 classifiable nodes, dispersal events were more frequent than vicariance events for all time slices (Table 3). Speciation by vicariance affected two clades in particular: the brachiopod genus *Plaesiomys* and the trilobite genus *Flexicalymene*.

3.1.1. Comparison with other geologic intervals

Although dispersal was the dominant speciation mode throughout all four temporal intervals, vicariance was also an important process that operated both within and among continents (Table 3, Fig. 5). The relative frequency of vicariance vs. dispersal differed among temporal bins, which is consistent with other analyses that have noted variation in the occurrence of vicariance vs. dispersal through geologic time (Stigall, 2010) or the alternation of vicariance and dispersal events within clades (Stigall et al., 2017). The high level of dispersal observed for the T1-T3 interval is similar to that reported during the Late Devonian Biodiversity Crisis, an interval of pervasive interbasinal-species invasion events (Stigall, 2010) that are comparable to the many long-distance dispersal events observed in this data set (Fig. 5). Ancestral range estimation using modern clades has also recovered shifting dispersal:vicariance ratios through geologic time. For example,

Table 2
Comparisons of model fits from the BioGeoBEARS analyses.

	Model[i]	lnL[a]	AIC[b]	AICc[c]	ΔAICc[d]	ωi[e]	*d*[f]	*e*[g]	*j*[h]
Bumastoides	DEC	− 41.66	87.32	88.65	2.70	0.09	0.130	1.2E − 01	0
	DEC + J	− 38.72	83.44	86.44	0.49	0.28	0.051	4.5E − 02	0.24
	DIVALIKE	− 40.31	84.62	85.95	0.00	0.36	0.130	6.2E − 02	0
	DIVALIKE + J	− 39.21	84.42	87.42	1.47	0.17	0.054	4.1E − 02	0.11
	BAYAREALIKE	− 45.75	95.50	96.83	10.88	0.00	0.270	2.8E − 01	0
	BAYAREALIKE + J	− 39.77	85.54	88.54	2.59	0.10	0.036	3.2E − 02	0.62
Deiphoninae	DEC	− 71.83	147.66	148.33	40.00	0.00	0.014	2.8E − 02	0
	DEC + J	− 51.49	108.99	110.40	2.07	0.19	0.001	1.0E − 12	0.14
	DIVALIKE	− 68.42	140.84	141.51	33.18	0.00	0.016	1.8E − 02	0
	DIVALIKE + J	− 50.46	106.92	108.33	0.00	0.55	0.000	1.0E − 12	0.27
	BAYAREALIKE	− 86.28	176.55	177.22	68.89	0.00	0.022	2.1E − 01	0
	BAYAREALIKE + J	− 51.20	108.40	109.81	1.48	0.26	0.000	1.0E − 07	0.22
Eochonetes	DEC	− 40.73	85.46	86.55	26.65	0.00	0.034	5.7E − 02	0
	DEC + J	− 26.44	58.88	61.28	1.38	0.31	0.000	1.0E − 12	0.12
	DIVALIKE	− 37.06	78.12	79.21	19.31	0.00	0.032	1.0E − 12	0
	DIVALIKE + J	− 25.75	57.50	59.90	0.00	0.62	0.000	1.0E − 12	0.12
	BAYAREALIKE	− 49.43	102.86	103.95	44.05	0.00	0.062	4.3E − 01	0
	BAYAREALIKE + J	− 27.87	61.74	64.14	4.24	0.07	0.000	1.0E − 07	0.13
Flexicalymene	**DEC**	− 37.63	79.26	80.35	0.00	0.75	0.019	1.0E − 12	0
	DEC + J	− 37.15	80.30	82.70	2.35	0.23	0.017	3.8E − 09	0.02
	DIVALIKE	− 41.80	87.60	88.69	8.34	0.01	0.029	1.0E − 12	0
	DIVALIKE + J	− 41.27	88.54	90.94	10.59	0.00	0.025	1.0E − 12	0.02
	BAYAREALIKE	− 55.09	114.18	115.27	34.92	0.00	0.033	2.5E − 01	0
	BAYAREALIKE + J	− 40.65	87.30	89.70	9.35	0.01	0.007	1.0E − 07	0.1
Glyptorthis	DEC	− 68.06	140.12	140.72	17.72	0.00	0.049	1.0E − 12	0
	DEC + J	− 57.87	121.74	123.00	0.00	0.92	0.019	1.0E − 12	0.16
	DIVALIKE	− 66.28	136.56	137.16	14.16	0.00	0.064	2.0E − 08	0
	DIVALIKE + J	− 60.49	126.98	128.24	5.24	0.07	0.028	1.0E − 12	0.11
	BAYAREALIKE	− 82.33	168.66	169.26	46.26	0.00	0.078	4.8E − 01	0
	BAYAREALIKE + J	− 62.21	130.42	131.68	8.68	0.01	0.020	1.0E − 07	0.13
Hebertella	DEC	− 23.06	50.12	51.83	1.85	0.18	0.066	1.0E − 12	0
	DEC + J	− 19.99	45.98	49.98	0.00	0.45	0.023	1.0E − 12	0.11
	DIVALIKE	− 22.72	49.44	51.15	1.17	0.25	0.071	1.0E − 12	0
	DIVALIKE + J	− 21.67	49.34	53.34	3.36	0.08	0.034	1.0E − 12	0.08
	BAYAREALIKE	− 30.46	64.92	66.63	16.65	0.00	0.071	1.3E − 01	0
	BAYAREALIKE + J	− 22.66	51.32	55.32	5.34	0.03	0.023	6.0E − 02	0.08
Homalonotidae	DEC	− 29.66	63.32	64.32	10.34	0.00	0.014	1.0E − 02	0
	DEC + J	− 23.95	53.90	56.08	2.10	0.23	0.003	1.0E − 12	0.07
	DIVALIKE	− 27.33	58.66	59.66	5.68	0.04	0.017	1.0E − 12	0
	DIVALIKE + J	− 22.90	51.80	53.98	0.00	0.66	0.004	1.0E − 12	0.06
	BAYAREALIKE	− 38.91	81.82	82.82	28.84	0.00	0.027	9.1E − 02	0
	BAYAREALIKE + J	− 25.12	56.24	58.42	4.44	0.07	0.002	1.0E − 07	0.08
Plaesiomys	DEC	− 37.36	78.72	80.43	5.68	0.04	0.059	1.2E − 02	0
	DEC + J	− 34.58	75.16	79.16	4.41	0.08	0.036	1.0E − 12	0.13
	DIVALIKE	− 34.52	73.04	74.75	0.00	0.70	0.063	2.4E − 08	0
	DIVALIKE + J	− 33.89	73.78	77.78	3.03	0.16	0.050	1.0E − 12	0.05
	BAYAREALIKE	− 47.85	99.70	101.41	26.66	0.00	0.110	3.9E − 01	0
	BAYAREALIKE + J	− 35.86	77.72	81.72	6.97	0.02	0.025	5.5E − 02	0.13
Tetralichinae	DEC	− 46.65	97.30	98.63	20.87	0.00	0.036	8.0E − 09	0
	DEC + J	− 34.57	75.14	78.14	0.38	0.34	0.009	1.0E − 12	0.94
	DIVALIKE	− 41.58	87.16	88.49	10.73	0.00	0.042	2.0E − 08	0
	DIVALIKE + J	− 34.38	74.76	77.76	0.00	0.41	0.010	1.0E − 12	0.43
	BAYAREALIKE	− 55.26	114.52	115.85	38.09	0.00	0.110	4.6E − 01	0
	BAYAREALIKE + J	− 34.87	75.74	78.74	0.98	0.25	0.008	1.0E − 07	0.79
Thaleops	DEC	− 63.94	131.88	132.63	22.19	0.00	0.051	1.0E − 12	0
	DEC + J	− 51.42	108.84	110.44	0.00	0.69	0.021	1.0E − 08	0.24
	DIVALIKE	− 62.32	128.64	129.39	18.95	0.00	0.068	4.9E − 08	0
	DIVALIKE + J	− 52.34	110.68	112.28	1.84	0.27	0.024	1.0E − 12	0.27
	BAYAREALIKE	− 80.05	164.10	164.85	54.41	0.00	0.078	2.5E − 01	0
	BAYAREALIKE + J	− 54.27	114.54	116.14	5.70	0.04	0.017	8.3E − 03	0.59

[a] Log-likelihood (lnL) values from the BioGeoBEARS analysis.
[b] Akaike Information Criterion (AIC).
[c] Corrected AIC (AICc).
[d] Difference in AIC values compared to best-fit models (ΔAIC).
[e] Akaike weight, the relative likelihood of model (ωi).
[f] Measure of dispersal rate along branches within each phylogeny.
[g] Measure of extinction rate along branches within each phylogeny.
[h] Measure of relative weight of jump dispersal.
[i] Best fit models are bolded and based upon the AICc values.

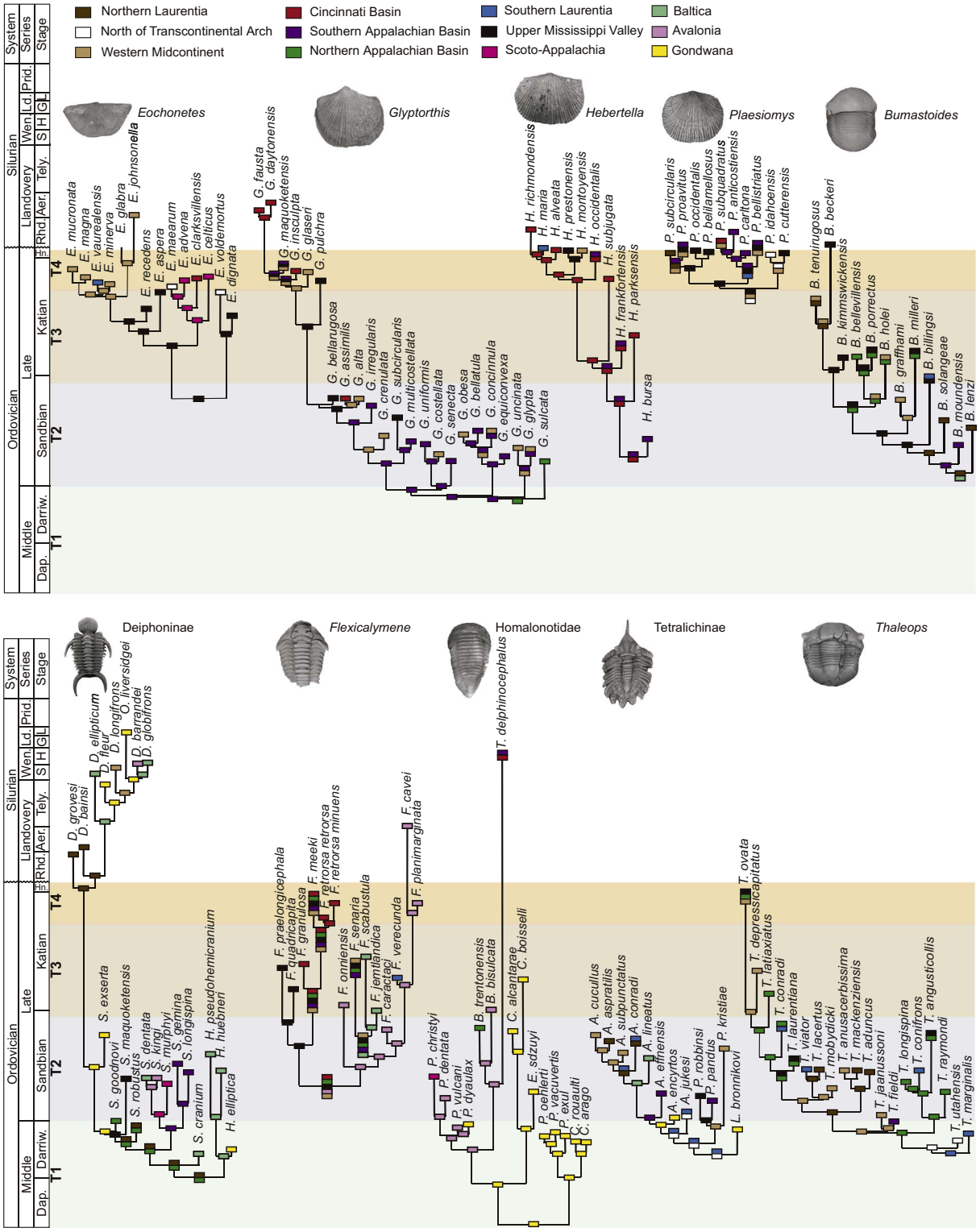

Fig. 4. Cladograms with ancestral range estimates for brachiopod and trilobite taxa using maximum likelihood inference with the R package BioGeoBEARS. Geologic ranges for each species can be found in Supplemental Table S1. Estimated geographic ranges are indicated by color boxes, which match area colors of Fig. 1. *Eochonetes clarksvillensis*, *Glyptorthis insculpta*, *Hebertella frankfortensis*, *Plaesiomys subquadratus*, and *Flexicalymene meeki* images from the Digital Atlas of Ordovician Life (Stigall et al., 2014). *Bumastoides milleri* image from Carlucci et al. (2012); *Sphaerocoryphe robusta* from Museum of Comparative Zoology, Harvard University (http://mcz.harvard.edu); *Trimerus delphinocephalus* from Congreve and Lieberman (2008); *Probolichas kristiae* from Carlucci et al. (2010); *Thaleops laurentiana* from Amati and Westrop (2004). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

clownfishes analyzed using BioGeoBEARS evolved primarily through dispersal events over the past 15 million years (BAYAREALIKE + J model) (Litsios et al., 2014). Similarly, Thacker's (2015) phylogeny of goby fish, analyzed under DEC + J, showed elevated dispersal events across the Eocene (vicariance, 12%; dispersal, 88%) and Oligocene (vicariance, 29%; dispersal, 71%). However, the Neogene had equal amounts of vicariance and dispersal speciation within the Gobiidae and Gobionellidae lineages. This may indicate that dispersal processes that

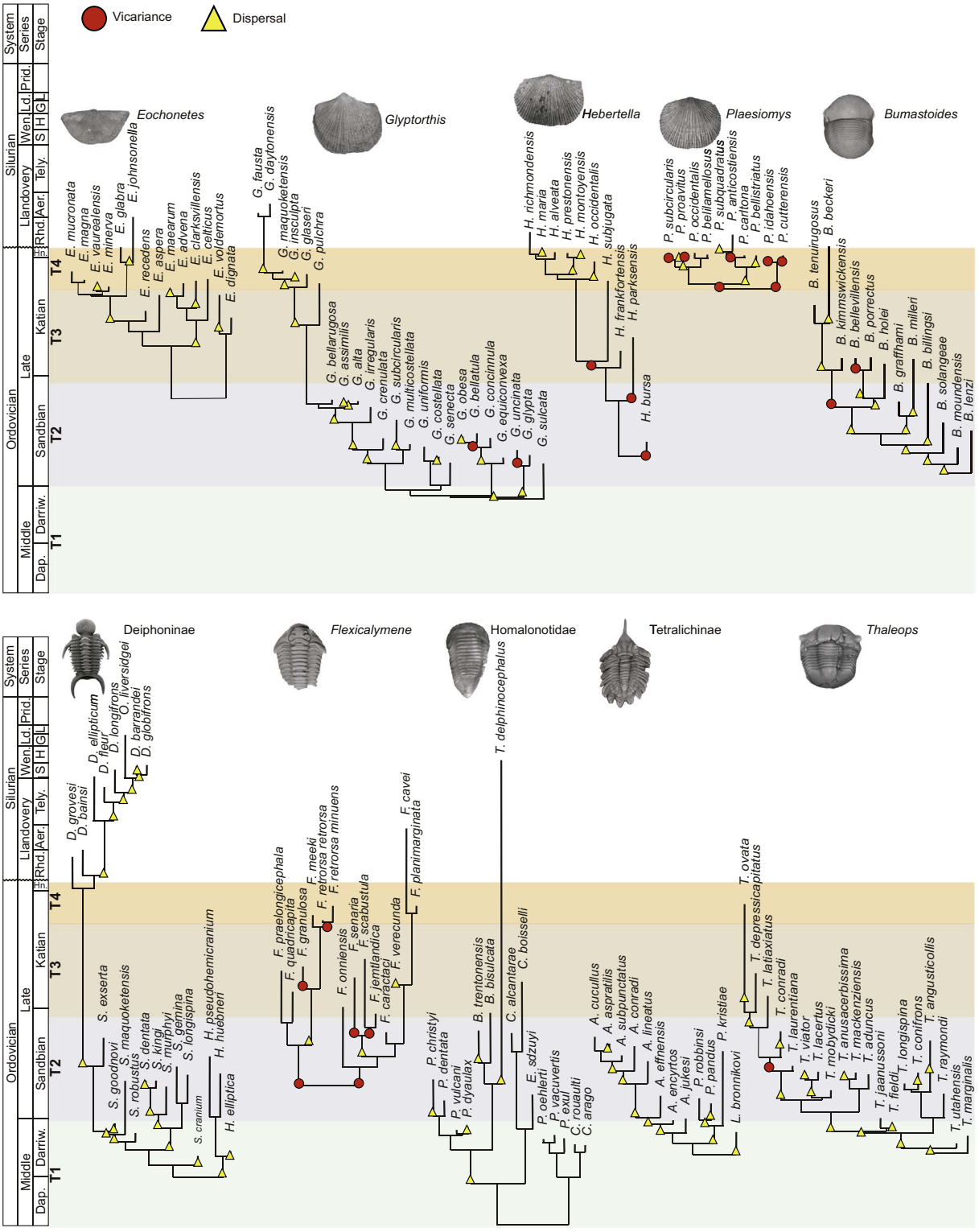

Fig. 5. Cladograms depicting speciation processes among brachiopod and trilobite taxa using maximum likelihood models generated within the R package BioGeoBEARS. Geologic ranges for each species can be found in Supplemental Table S1. Image attributes as in Fig. 4.

operated in the Middle through Late Ordovician were similar to processes operational across island clades during the Eocene and Oligocene, times in which sea level was generally more elevated compared to the Neogene (Miller et al., 2005) and would thus have been conducive to dispersal processes. More in-depth paleobiogeographic analyses of Ordovician and Cenozoic clades are needed to further elaborate similarities and differences among biogeographic drivers of evolution through Earth history.

3.2. Area relationships and dispersal patterns

3.2.1. T1 time slice

The Middle Ordovician T1 time slice, which incorporates the GOBE, is characterized by dispersal speciation only. The BioGeoBEARS results for the T1 time slice suggest substantial dispersal among Gondwana, Avalonia, Baltica, and Laurentia within the Deiphoninae, Tetralichinae, Homalonotidae, *Thaleops*, and *Glyptorthis* clades (Fig. 4, Fig. 5). Most of

Table 3
Distribution of cladogenetic events (raw count with percent in parenthesis).

	Brachiopods			Trilobites			Total	
Time slice	Dispersal	Vicariance	Total	Dispersal	Vicariance	Total	Dispersal	Vicariance
T4	13 (65%)	7 (35%)	20	0 (0%)	0 (0%)	0	13 (65%)	7 (35%)
T3	7 (87%)	1 (13%)	8	4 (57%)	3 (43%)	7	11 (73%)	4 (27%)
T2	9 (69%)	4 (31%)	13	30 (83%)	6 (17%)	36	39 (80%)	10 (20%)
T1	2 (100%)	0 (0%)	2	20 (100%)	0 (0%)	20	22 (100%)	0 (0%)

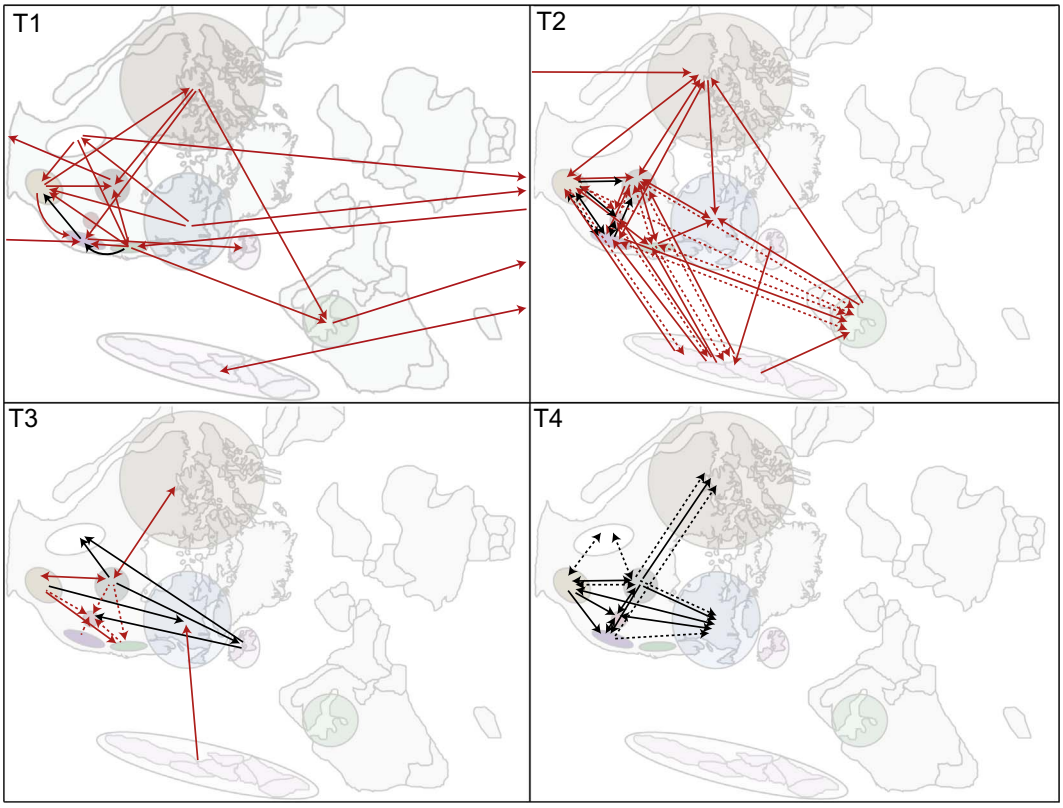

Fig. 6. Pathways and basin associations reconstructed from maximum-likelihood analyses for brachiopod (black lines) and trilobite (red lines) clades. Arrows indicate dispersal direction, with solid lines representing dispersal events and dashed indicating vicariance events. Double-headed arrows indicate that dispersal or vicariance happened between two areas during the same time slice, but not necessarily in the same clade. Single dispersal and vicariance events that took place among several basins are drawn as separate events to capture the relationships among areas. In the T1 and T2 time slices, dispersal between Laurentia and Gondwana was reconstructed to cross the Paleo-Tethys ocean when Gonwanan taxa occupied the western portion of the continent, but to cross the opposite direction when Gondwana taxa occupied the eastern portion of the continent. Paths drawn do not necessarily reflect the true dispersal path, but should be viewed as the general direction in which dispersal occurred. See Fig. 1 for area names. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the recovered dispersal routes were either intra-Laurentian or were from Laurentia to other paleocontinents (Fig. 6). The focus on Laurentia occurs as a by-product of taxon selection (see Methods), nevertheless the evidence for significant dispersal pathways involving other paleocontinents is notable.

Continents were at their maximum dispersion during the T1 time slice relative to the other time slices (Cocks and Torsvik, 2002). However, the T1 interval includes the greatest number of long-distance dispersal routes in the dataset, principally among trilobites, which indicates substantial potential for transoceanic dispersal at this time. Dispersal occurred from Laurentia to Gondwana and vice versa, between Gondwana and Avalonia, from Baltica to Gondwana, and from Laurentia to Baltica and Scoto-Appalachia. Most of these long-distance dispersal events were in an easterly direction, but some dispersal events were westerly as well.

Like later intervals, the T1 time slice was characterized by significant dispersal among Laurentian basins, except the Cincinnati and Scoto-Appalachian basins. Trilobite dispersals occurred in all directions, but the primary pathways were counter-clockwise around central Laurentia or oriented centrally toward the Upper Mississippi Valley. The two brachiopod dispersal paths both indicate a west to northwest dispersal direction (Fig. 6).

3.2.2. *T2 time slice*

The T2 time slice, which encompasses the majority of the Late Ordovician Sandbian Age including the Bloutian tectophase of the Taconian Orogeny, contains the greatest number of speciation events and includes both dispersal and vicariance events (Table 3). Compared to the T1 time slice, dispersal events between paleocontinents remained frequent, but the locus of dispersal shifted away from Gondwana and increased among paleocontinents bordering the Iapetus, principally Laurentia, Baltica, and Avalonia. Among dispersal routes, there is a strong dominance of southeast to northwest dispersal from Avalonia and Baltica into Laurentia. Frequent vicariance events are also recorded among the circum-Iapetus continents. As with the T1 time slice, both intra-Laurentian and inter-continental events were common in trilobite

clades, but all speciation events within brachiopod lineages occurred within Laurentia.

Within our dataset, inter-continental speciation events were restricted to the Holamonotidae, Deiphoninae, Tetralichinae, and *Flexicalymene* clades (Fig. 5). Episodes of dispersal were recovered from Gondwana to Laurentia, Scoto-Appalachia to Avalonia, Laurentia to Avalonia and Baltica, Avalonia to Baltica and Laurentia, and Baltica to Laurentia (Fig. 6). Although dispersal was the most frequent speciation type in these clades, vicariance also occurred. Notably, the *Flexicalymene senaria* clade records a two-step vicariance of Baltica separating from Avalonia and then Laurentia. Trilobite clades also record speciation events occurring within Avalonia, Baltica and Gondwana.

The Tetralichinae, *Flexicalymene*, *Thaleops*, *Glyptorthis*, and *Hebertella* clades exhibit intra-Laurentian speciation. Many of these events are dispersal events; indeed, these events record bidirectional exchange between most Laurentian basins and lack a discernable preferred directionality. Northern Laurentia did not directly exchange taxa with the Cincinnati basin or the Northern Appalachian basin. Instead, dispersal of taxa between these areas was mediated by initial dispersal through more central areas, either the Upper Mississippi Valley or Southern Laurentia. The centrally located basins were also the locus of vicariance speciation within Laurentia. This combination of dispersal and vicariance among the same basins suggests alternating intervals of dispersal and vicariance, such as described in the Biotic Immigration Event (BIME) model of Stigall et al. (2017). Alternation of vicariance and dispersal speciation is most evident within *Glyptorthis* (e.g., the *G. obesa* lineage) and *Flexicalymene* (e.g., the *F. senaria* lineage) (Fig. 5).

3.2.3. T3 time slice

The T3 time slice is characterized by the Taconic tectophase of the Taconian Orogeny, which produced increased tectonic stress on the eastern margin of Laurentia and caused a switch from tropical to temperate carbonate deposition in the southern margin basins. Except for a single dispersal event from Avalonia to Southern Laurentia, all dispersal and vicariance events of the T3 time slice occurred among Laurentian basins. Dispersal events, in general, occurred less frequently than during the T1 and T2 time slices (Table 3, Fig. 6).

Two primary biogeographic pathways operated within Laurentia: a central pathway linking basins via the Upper Mississippi Valley region and a southern pathway from the Western Midcontinent to Cincinnati and the Appalachian basins (Fig. 6). Along the central pathway, dispersal events were numerous and took place between the Upper Mississippi Valley into the Western Midcontinent, North of the Transcontinental Arch, Northern Laurentia and Scoto-Appalacian areas. Vicariance also occurred when widespread taxa previously inhabiting multiple areas (Upper Mississippi Valley, Southern Appalachian basin, Cincinnati basin, Northern Appalachian basin, and Western Midcontinent) were isolated to form new species (Fig. 5). Similar to the T2 time slice, vicariance and dispersal events alternated within lineages. Some T3 vicariance events, such as those within *Bumastoides* (e.g., *B. bellevillensis*), occur secondary to a dispersal event in the T2 time slice. Another *Bumastoides* lineage (*B. tenuirugosus*) exhibits a T3 dispersal event following a vicariance event in the T2 time slice (Fig. 5).

3.2.4. T4 time slice

The Late Ordovician T4 interval includes the Richmondian Invasion and is characterized by the return of tropical carbonate deposition in the southern margin basins of Laurentia, and decreased distances among Laurentia, Avalonia, and Baltica as the latter two continents continued migrating north and northwest, respectively (Torsvik and Cocks, 2013). Speciation frequency was lower during the T1 and T2 time slices, but slightly higher during the T3 time slice.

Speciation was limited to the four brachiopod clades within Laurentian basins during this time slice. Biogeographic patterns are similar to the overall patterns of the T3 time slice. The northern and southern pathways were still present, although dispersal between the Cincinnati basin and other areas was substantially greater than in previous intervals (Fig. 6). During this interval, which includes the Richmondian Invasion, taxa dispersed into the Cincinnati basin from Southern Laurentia, Southern Appalachia, the Western Midcontinent, and the Upper Midwest. This is a notable change from the T3 time slice, during which the Cincinnati region was biogeographically isolated and most Cincinnati area speciation events involved vicariance. All four brachiopod genera speciated via dispersal during the T4 time slice, but only *Plaesiomys* exhibited substantial vicariance. Neither *Eochonetes* nor *Hebertella* have widely dispersed T4 taxa, which precludes potential for vicariance in these clades during this interval. As with other clades in previous intervals, dispersal and vicariance events alternate within *Plaesiomys* (*P. subcircularis* lineage), which supports an alternation of dispersal and vicariance processes linking and subsequently isolating the Laurentian basins during this time slice.

4. Discussion

The evolution and biogeography of Middle to Late Ordovician brachiopods and trilobite lineages analyzed were controlled by both biotic and abiotic factors, the importance of which varied through time. Analysis of these factors provides a context to examine how interactions between biology, ocean currents, climate, and tectonics can impact the evolution of clades, and particularly provides a context to consider how changes in the Earth system may impact the evolution of clades at other times in Earth's history.

4.1. Biotic influences on speciation and dispersal patterns

Larval ecology has been shown to play a critical role in dispersal distance and patterns within marine invertebrates (Treml et al., 2015; Sorte, 2013). Because adult brachiopods are sessile organisms, dispersal must occur during the larval state (Rudwick, 1970; Freeman and Lundelius, 2005; Muñoz and Benedetto, 2016). Similarly, the incorporated trilobite clades had adult phases with limited home ranges (Chatterton and Speyer, 1989), supporting a role for larval dispersal. Thus, dispersal patterns observed within this study must be at least partly attributed to larval type, time spent in the larval phase, and/or larval position in the water column.

Studies of Paleozoic articulated brachiopods indicate these organisms produced large larval shells (protegulum) that are common among planktotrophic organisms, which suggests that Late Ordovician articulate brachiopods had planktotrophic larvae (Valentine and Jablonski, 1983; Freeman and Lundelius, 2005). Planktotrophic larvae are self-feeding forms capable of spending weeks to months in a larval phase (Jablonski and Lutz, 1983). Today, self-feeding larval forms have high dispersal potential under adequate oceanographic conditions. Modeling studies of Caribbean fish populations recovered dispersal on the scale of 10 to 100 km in one generation before larval settlement facilitated by local currents (Cowen et al., 2006). Similarly, studies examining dispersal of planula (self-feeding) larvae of tropical Pacific scleractinian coral species identified dispersal of 50 to 150 km in a single generation before settlement (Treml et al., 2008). In addition, Lam and Stigall (2015) found that the majority of invasive taxa into the Cincinnati Basin during the Late Ordovician Katian Age had planktotrophic larvae capable of long-distance dispersal, which suggests that Ordovician taxa likely exhibited dispersal capacities similar to modern analogs.

Trilobites exhibit a variety of larval types related to their complex life cycle (Chatterton and Speyer, 1989; Hughes et al., 2006; Park and Choi, 2011). Planktic larval stages have been previously proposed for some of the trilobites included in this study, notably *Flexicalymene* (Chatterton and Speyer, 1989; Crônier et al., 2011). Three clades, the Deiphoninae, Homalonotidae, and Tetralichinae, trilobites, have been hypothesized to have had a planktic-benthic larval life strategy (Chatterton and Speyer, 1989; Congreve and Lieberman, 2010). However, two trilobite clades examined in this study, *Bumastoides* and

Thaleops, belong to families previously hypothesized to have dominantly benthic larval phases (Chatterton and Speyer, 1989).

Compared to planktic larvae, the dispersal potential of benthic larvae is lower. Therefore, one would expect the dispersal potential of brachiopods, in general, to be higher than trilobites, and exhibit increased intercontinental dispersals. However, this expectation is neither indicated nor statistically supported in this dataset. Instead, trilobites exhibit the highest number of long-distance (i.e., intercontinental) dispersal events, notably in the T1 and T2 time slices. Brachiopod dispersal is mostly confined to Laurentia and its marginal Scoto-Appalachian basin. This is partly due to clade selection during construction of the phylogenetic hypotheses, and thus additional brachiopod phylogenies containing cosmopolitan taxa are required to determine if brachiopods exhibited long-distance dispersal out of Laurentia. Nonetheless, a clear biogeographic signal in the trilobite clades indicates that although some of the organisms possessed benthic larval states (e.g., tetralichine trilobites that dispersed from Laurentia to Gondwana in the T1 time slice), they were not inhibited by a shorter time spent as larvae. Our results indicate that the majority of trilobite species used within this study possessed larvae that were capable of longer-distance dispersal. Notably, the deiphonine trilobites, a clade with hypothesized planktic larvae (Chatterton and Speyer, 1989; Congreve and Lieberman, 2010), exhibited species migration from Baltica to Gondwana and from Laurentia to Gondwana in the T1 time slice, and from Avalonia to Baltica and Laurentia to Avalonia in the T2 time slice.

Dispersal in trilobite taxa with benthic larvae was likely accomplished via long-distance founder-event speciation, as their larvae would not have been affected as greatly by surface currents as planktotrophic larvae. The hypothesis that an evolutionary advantageous 'island hopping' strategy was utilized is supported by the support for the "+J" model variants (Table 2). Brachiopods, namely *Eochonetes* and *Glyptorthis*, also utilized this strategy to disperse among Laurentian basins. This indicates a key role for jump dispersal and founder-event speciation within the evolution of the focal clades.

Previous studies of Ordovician taxa further support the importance of founder-event speciation in Paleozoic clades. For example, islands arcs were previously identified as "stepping stones" between paleogeographic areas suitable for larval growth and development by Neuman (1972). "Island-hopping" was also proposed by Congreve and Lieberman (2008) as an explanation for dispersal among Laurentia, Avalonia, and Arabia (Southern Gondwana) in the Homalonotidae trilobites. McKerrow et al. (2000) concluded the oceans separating continents were < 1000 km wide during the Ordovician and suggested that dispersal of organisms across oceans during the Late Ordovician were plausible. However, subsequent analyses by Lees et al. (2002) estimated substantially wider oceans. Even with significantly wider oceans separating shallow water habitats, larval dispersal could have been facilitated by the abundant volcanic island arc chains with suitable shallow water habitat that surrounded subduction zones of Laurentia, Baltica, Avalonia, and Gondwana.

Notably, dispersal and vicariance events between brachiopods and

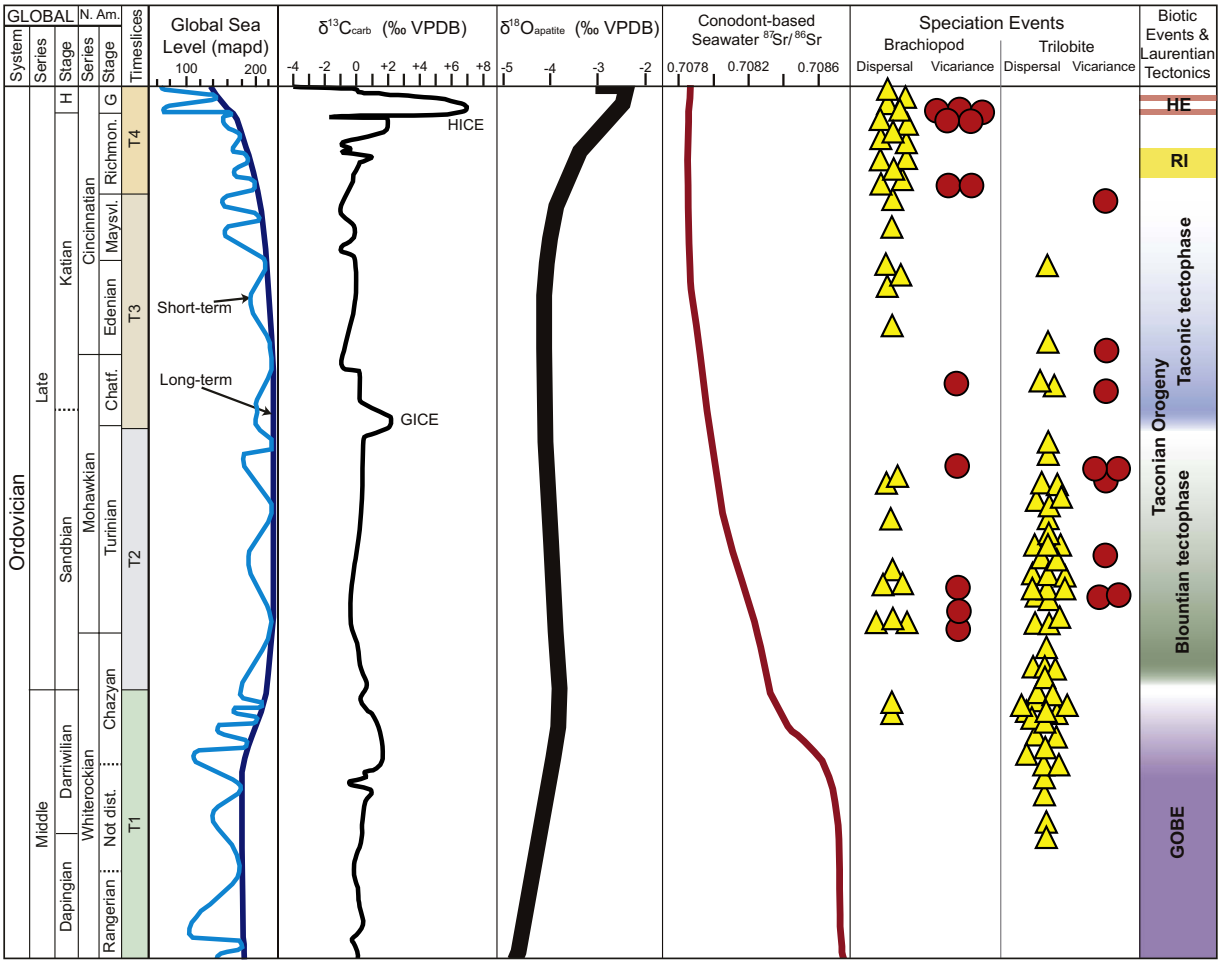

Fig. 7. Chronostratigraphy, time slices used throughout this study, sea-level, geochemical proxies, biotic events, and tectophases of the Taconian Orogeny graphed with brachiopod and trilobite speciation events (from Fig. 5). RI, Richmondian Invasion (Cincinnati basin); HE, Hirnantian Extinctions; mapd, meters above present-day sea level. Global sea-level curves from Haq and Schutter (2008); generalized $\delta^{13}C$ carbonate curve from Bergström et al. (2009); $\delta^{18}O$ apatite curve from Trotter et al. (2008), and North American seawater strontium values from Edwards et al. (2015).

trilobites were largely synchronous through the early Sandbian to early Katian ages (Fig. 7). This indicates that although some trilobites possessed benthic protaspid phases, larval types of the focal taxa responded similarly to tectonic, paleoclimate, and paleoceanographic events. Thus, larval type and time spent in a larval state were important factors that affected the dispersal patterns between brachiopods and trilobites within this data set.

4.2. Paleoceanographic and tectonic influences on species dispersal

Ascertaining extrinsic causal mechanisms for species dispersal requires examining the recovered pathways in light of published paleoclimatic and paleoceanographic reconstructions for the Middle through Late Ordovician. The connections among continents were compared to the surface ocean circulation models of Pohl et al. (2016b) for the Middle Ordovician (460 Ma) interval. Although the authors created ocean circulation models for three time slices for three different CO_2 scenarios that span the Early Ordovician to Early Silurian, we only use the Middle Ordovician model created under 8 PAL because major ocean gyres and currents within the Middle Ordovician model are still present and relatively unchanged in the Early Silurian model. In addition, CO_2 concentrations were found to have little effect on the position of ocean currents and gyres in the Middle Ordovician, and 8 PAL is considered a conservative, intermediate value (Pohl et al., 2016b). We acknowledge that during the study interval, the paleolatitudinal distances among continents likely changed significantly (Torsvik et al., 2012). However, because of taxon selection in the T3 and T4 time slices of the Late Ordovician, most taxa are confined to Laurentian basins and paleodistance among continents is, therefore, not a substantial factor in dispersal analysis of these time slices.

4.2.1. Middle Ordovician T1 time slice

During the Dapingian to Sandbian ages of the Middle Ordovician T1 time slice, which includes the GOBE interval, several dispersal events were identified among Laurentia, Avalonia, and Gondwana within trilobite lineages (Fig. 6).

Three dispersals took place from Laurentia into Gondwana within the trilobite lineages *Amphilichas encyrtos* (into New South Wales and Tasmania; northeastern margin of Gondwana), *Sphaerocoryphe exserta* (into New South Wales; northeastern margin of Gondwana), and *Lyralichas bronnikovi* (into Kazakhstan). Dispersal from Laurentia into Gondwana and the Kazakh terranes was accomplished via equatorial currents and large oceanic gyre systems.

Dispersal from Laurentian basins into New South Wales in the *S. exserta* lineage, a deiphonine trilobite with a planktic larval phase, could have been accomplished via the North and South Equatorial currents, as well as the North Panthalassic convergence. Dispersal from Laurentia into Gondwana within the *A. encyrtos* lineage, a tetralichine trilobite hypothesized to have an alternate planktic larval form (Chatterton and Speyer, 1989), was likely aided by the same currents and gyre systems. Dispersal of this lineage across the Panthalassa Ocean, which lacked abundant volcanic island arcs and shallow carbonate platforms compared to the Paleo-Tethys, is further support for a planktic larval stage. Thus, long distance founder-event speciation is invoked to explain the great dispersal distance exhibited by this lineage.

Determining the dispersal mechanisms for *L. bronnikovi* from Southern Laurentia and North of the Transcontinental Arch is complicated and premature, as this species' occurrence information in the strata of Kazhakstan is severely lacking. Therefore, at this time we do not attempt to interpret the dispersal history of this species from Laurentia into the Kazakh terranes.

Strong hurricane activity, originating around 10°S of the equator that swept across Laurentia from the northeast to southwest (Poussart et al., 1999; Jin et al., 2013) (Fig. 2), would have further helped to push deiphonine and tetralichine trilobites that originated in the Laurentian Upper Mississippi Valley and northern Laurentian basins, respectively, southward into the influence of the North and South Equatorial current and/or the North Panthalassic convergence. Storms and hurricanes have been observed in modern clades to greatly influence larval dispersal distance (Radford et al., 2014). Several island arcs that surrounded the northern and southern margins of the Iapetus Ocean on the Laurentian and Avalonian platforms (McKerrow and Cocks, 1986; Mac Niocaill et al., 1997) would have also aided in dispersal of benthic trilobite larvae across vast ocean basins via long-distance founder-event speciation.

Several dispersal events took place among Laurentian basins during the Middle Ordovician (Table 3, Fig. 7). Trilobite dispersal patterns appear random, with no preference for a dispersal direction (Fig. 6). This was likely due in part to elevated sea-level during the latest Darriwilian, which allowed for breaching of physical barriers by larvae (Patzkowsky and Holland, 1996; Haq and Schutter, 2008). Dispersal within *Thaleops* lineages from the Western Midcontinent to the Southern Appalachian basin was promoted by the counter-clockwise flowing Southern Laurentian Current (SLC) (Fig. 1). Lineages of *Glyptorthis* brachiopods dispersed from the Northern Appalachian basin west into the Southern Appalachian basin, with subsequent dispersals northwest into the Western Midcontinent basin (Fig. 6). This dispersal pattern is correlative to infilling of a portion of the Southern Appalachian basin, particularly southwestern Virginia, with a switch from a shale- limestone facies to clastic deposition and eventual filling of the basin in the Middle Ordovician (Read, 1980). Localized surface currents or coastal upwelling zones resulting from the movement of prevailing winds along a shoreline caused offshore movement of surface waters due to Eckman transport and were likely responsible for dispersal of brachiopod larvae out of the Southern Appalachian basin into more favorable facies. Additional influence of the SLC on dispersal patterns is evident within *Plaesiomys* lineages as species dispersed between the Western Midcontinent and Southern Appalachian basins (Figs. 5, 6).

The T1 time slice is characterized by speciation events due to dispersal only (Table 3), which suggests that physical and thermal barriers between geographic regions were not substantial obstacles for larval dispersal between basins within this dataset. This is especially evident within Laurentia, as dispersal occurred in all directions. In addition, geochemical studies indicate global cooling during this interval (Trotter et al., 2008), which coincided with increased biodiversity pulses (Fig. 7). This pattern is also manifested within trilobite lineages, as numerous speciation events occurred during intervals of global cooling. This result matches with previous studies showing increased diversification rates during the Middle Ordovician GOBE interval (Miller and Foote, 1996; Droser and Finnegan, 2003; Harper, 2006). In addition, the pattern of increased speciation during intervals of global cooling has been noted for planktic foraminifera and crustaceans throughout the Neogene during the growth of Antarctic and Northern Hemisphere ice sheets (Fraass et al., 2015; Davis et al., 2016). Cooling would have caused an increased temperature gradient between polar and equatorial regions, leading to increased wind strength over the oceans (Brown et al., 2001; Rasmussen et al., 2016). This may have resulted in an intensification of wind-driven ocean currents and gyre systems in the Middle Ordovician, thus leading to increased dispersal mechanisms for benthic invertebrate larvae. Similarly, Baarli et al. (2017) proposed that cooling oceans and intensification of gyre systems following the formation of late Neogene polar ice caps promoted dispersal in North Atlantic planktotrophic barnacle species.

4.2.2. Early Late Ordovician (Sandbian-M4/M5 sequence boundary) T2 time slice

The T2 time slice, encompassing the majority of the early Late Ordovician Sandbian Age, included several dispersal events and elevated speciation by vicariance compared to the T1 time slice (Table 3). This time interval was characterized by the beginning of the Blountian tectophase of the Taconian Orogeny on the southern margin of Laurentia (Fig. 7). The recovered dispersal from Gondwana into the

Northern Laurentian basin (western Canada) was likely aided by the counter-clockwise south Paleo-Tethys convergence and the North and South Equatorial currents that flowed westward (Fig. 1). Two dispersal events in trilobite lineages that took place from Baltica into the Northern and Southern Laurentian basins were likely facilitated by the decreased width of the Iapetus Ocean and volcanic island arcs surrounding the paleocontinents. The ocean circulation models of Pohl et al. (2016b) indicate that a small counter-clockwise gyre system flowed between Laurentia and Baltica, which–along with island arcs–-would have aided in species dispersal between these areas. In addition, an increased number of dispersal events from Avalonia into southern margin basins of Laurentia are observed during this time slice. Throughout this time, Avalonia was moving closer to Laurentia and Baltica as the Iapetus and Tornquist seas closed (Cocks and Torsvik, 2011). This likely caused Avalonia to move into warmer temperatures similar to those found on the southern margin of Laurentia, which would have facilitated dispersal of Avalonian lineages of trilobites into southern Laurentia via habitat tracking. Homogenization of faunas during the Sandbian has been identified in brachiopod lineages among Baltica, Laurentia, and Avalonia as the three paleocontinents moved closer together through the Sandbian (e.g., Hansen and Harper, 2007).

Vicariance events between Baltica and southern and western Laurentian basins were likely facilitated by increased tectonic activity during this time, as evidenced by the decreasing $^{87}Sr/^{86}Sr$ values (Fig. 7), which would have enhanced barriers including subaerially exposed arches, deep-water forearc basins, and/or structural depressions between paleobiogeographic basins, especially on the southern margin of Laurentia (Cracraft, 1985). Barriers would have restricted dispersal among southern margin basins; however, several dispersal events from Avalonia into the Southern and Northern Appalachian basins indicate that emplaced barriers may have acted to block dispersal from the east while allowing dispersal from the south.

Within Laurentia, dispersal occurred among all basins, with the exception of North of the Transcontinental Arch, with most dispersal events taking place into the Western Midcontinent and Upper Mississippi Valley. Dispersal into or from North of the Transcontinental Arch basin was likely hindered by its namesake, the Transcontinental Arch, a series of tectonically-rejuvenated structural highs that trended northeast-southwest across the midcontinent of Laurentia (reviewed in Carlson, 1999) (Fig. 2). Separate early middle Sandbian vicariance events in the brachiopod lineages of *Glyptorthis* and *Hebertella* indicate the Southern Appalachian basin became separated from both the Cincinnati basin and the Western Midcontinent. This signal indicates that barriers between the Cincinnati basin and Appalachian area were being emplaced throughout the later phase of the Blountian tectophase, and that the Transcontinental Arch or other intracratonic highland areas shielded dispersal from southern basins.

4.2.3. Late Ordovician (late Sandbian to mid-late Katian) T3 time slice

The T3 time slice is characterized dominantly by brachiopod dispersal and trilobite vicariance events (Table 3). After a brief quiescent period following the Blountian tectophase, the Taconic tectophase began with the locus of activity shifted toward the New York promontory (Shanmugam and Lash, 1982; Ettensohn, 1994; Fig. 7), which would have led to rejuvenation of intracratonic highlands and barriers. Emplacement of intracratonic barriers between the Northern Appalachian basin with surrounding basins is evident in vicariance events that took place within *Bumastoides* and *Flexicalymene* trilobite lineages.

Increased tectonic activity on the southern margin of Laurentia led to the initiation and deepening of the Sebree Trough. Introduction of cooler oceanic waters from the Iapetus Sea led to a sedimentological switch from tropical to temperate water carbonates at the M4/M5 sequence boundary within southern Laurentian basins, from the Southern Appalachian basin north into Quebec (Keith, 1989; Lavoie, 1995; Ettensohn, 2010). The switch was accompanied by increased abundance and distribution of siliciclastic sediments and more widespread distribution of phosphatic rocks (Patzkowsky et al., 1997). These lithologic changes have been interpreted to suggest increased turbidity, nutrient levels, and decreased water temperatures within this region (Lavoie, 1995; Holland and Patzkowsky, 1996, 1997; Pope and Read, 1997). In addition, the Guttenberg $\delta^{13}C$ (GICE) excursion took place within this interval, which some authors have interpreted to be from increased upwelling and productivity (Young et al., 2005). Associated with these changes were several vicariance events within trilobite lineages and one brachiopod dispersal that took place into the Cincinnati basin from the Southern and Northern Appalachian basins, Western Midcontinent, Upper Mississippi Valley, and the peri-cratonic Scoto-Appalachian basin. The elevated vicariance signal in trilobites compared to brachiopods in this timeslice indicates that environmental factors affected trilobite and brachiopod larvae differently within Laurentia. This may reflect larval type differences; however, vicariance and dispersal data points are limited, and more information is needed to conclusively determine if benthic and planktic larval types were affected differently. Dispersal was likely aided by strong storm activity as previously discussed, as well as upwelling zones developed on the margins of the Sebree Trough. Vicariance between the Western Midcontinent, Upper Mississippi Valley, Southern and Northern Appalachian basins and the Cincinnati Basin was likely accomplished via the emplacement of barriers between basins or the shift from tropical to temperate carbonates in the Cincinnati basin which could have ended successful migration and settlement of trilobite larvae. One speciation event into the Scoto-Appalachian basin and two out of the basin took place within the brachiopod genus *Eochonetes*, which indicates that the Scoto-Appalachian Basin may share closer faunal affinities with epicontinental basins than previously considered (cf. Bauer and Stigall, 2014).

Previous authors have noted that geographic range restrictions and extinctions occur in conjunction with lithologic changes caused by the introduction of cool waters into Laurentia (reviewed in Patzkowsky and Holland, 1993). Our analysis agrees with these interpretations, as several vicariance events are observed on the southern margins of Laurentia within trilobite clades. The Southern and Northern Appalachian basins and the Cincinnati basin are characterized by vicariance speciation events that separated these basins from basins located to the north. Dispersal events within brachiopod and trilobite clades are dominantly confined far to the east and north of the southern margin basins that were involved in the Taconian Orogeny.

4.2.4. Late Ordovician (Late Katian to Hirnantian) T4 time slice

During the late Katian to Hirnantian ages of the Late Ordovician T4 time slice, dispersal is observed exclusively within the brachiopod genera *Plaesiomys*, *Hebertella*, *Eochonetes*, and *Glyptorthis*. This time interval is associated with the return of tropical carbonate deposition in the southern margin basins of Laurentia due to the global warming interval known as the Boda Event (Holland and Patzkowsky, 1996; Holland, 1997; Fortey and Cocks, 2005), or to the cessation of cool Iapetus waters that infiltrated the craton through the Sebree Trough that was beginning to become filled by the Maysvillian Age (Ettensohn et al., 2002). Infilling of the trough would have led to the eventual cessation of midcontinent counter-clockwise circulation patterns (Kolata et al., 2001). The sedimentological change from temperate to tropical carbonate deposition likely facilitated the dispersal of brachiopods into the Cincinnati basin, as species could establish communities within newly favorable habitats. Hurricane activity during the Late Ordovician was especially strong, as several tempestite and “cornflake” beds recorded from the Cincinnati basin indicate regional-scale hurricane or tsunami events (Holland and Patzkowsky, 1996; Aucoin and Brett, 2015). The dispersal of *Glyptorthis* larvae from the Western Midcontinent into the Southern Appalachian basin and Cincinnati basin could have been assisted by storm activity. In addition, a major transgression took place at the Richmondian Age C5 sequence boundary of the Cincinnati basin (Holland, 1997). Hurricanes and

elevated sea-levels could have also promoted the longer-distance dispersal from midcontinent basins into Southern Laurentia (Fig. 2) within species of *Plaesiomys* and *Hebertella*, as there is a strong biogeographic signal that several speciation events occurred into this basin. Dispersal in an eastern direction into Southern Laurentia could have been accomplished as basins were infilled, removing physical and thermal barriers (e.g., the Transcontinental Arch and deep-water Maquoketa belt) among basins (Copper and Grawbarger, 1978; Elias, 1983).

During the Late Ordovician, Laurentian brachiopods exhibit a greater proportion of vicariance events than during other intervals (35% vicariance vs. 65% dispersal) (Fig. 6), all of which are concentrated around the early Hirnantian Age and a major eustatic regression (Fig. 7). This sea-level change likely inhibited dispersal from the southern margin basins (Cincinnati basin, Northern and Southern Appalachian basins) with North of the Transcontinental Arch and Southern and Northern Laurentia in some species. Previous analyses have linked the Late Ordovician mass extinction events with global cooling, increased ice volume on Gondwana, and related lowering of sea-level that would have eliminated shallow shelf areas and crucial niche space for marine organisms (Brenchley, 1988; Brenchley et al., 1994; Benton, 1995; Sepkoski, 1997; Finnegan et al., 2011; Harper et al., 2014). However, this study indicates that, although there is unrefuted evidence for biodiversity decline in many clades during the Hirnantian glaciation, speciation continued within these brachiopod clades and thus some clades were unaffected by loss of shallow shelf space.

4.3. Temporal trends in biogeographic drivers

Principal drivers of biogeographic patterns and speciation type shifted during the four Middle to Late Ordovician time slices. During the T1 and T2 time slices, climatic shifts and ocean gyres exerted primary controls over biogeographic patterns, particularly on inter-continental dispersal patterns. As inter-continental dispersal declined in later intervals, tectonic uplift and regional upwelling patterns within Laurentia became the primary drivers of biogeographic structure. This temporal shift reflects both a shift in the Earth system and evolutionary changes in the focal taxa, as “life and earth evolve together” (Croizat, 1964).

During the Middle Ordovician, global cooling has been linked to biodiversification pulses (Trotter et al., 2008), a correlation supported in this dataset by the elevated percent of dispersal events in trilobite lineages (Table 3, Fig. 7). Most of the trilobite clades utilized long-distance founder-event speciation (Table 2), presumably aided by the abundance of island arcs surrounding paleocontinents and surface currents. In addition, vicariance and dispersal events between brachiopods and trilobites are mostly synchronous. This implies three main points: 1) that increased diversity of organisms during the GOBE correlates with the spin-up of gyre systems and ocean currents due to global cooling, as suggested by Rasmussen et al. (2016) (Fig. 7), which may have been essential to organismal dispersal mechanics during this time interval; 2) because several trilobite lineages that exhibit long-distance dispersals, some which were previously hypothesized to have primarily benthic or an alternative planktic/benthic larval phase, likely exhibited planktic larval phases; and 3) larval type and time spent in a larval phase are important factors that affected dispersal patterns of benthic invertebrates.

Speciation events within Laurentia were influenced by tropical storm activity and surface currents across the entire study interval. Intense upwelling zones created by the Sebree Trough prevailed from the late Sandbian to the early Katian, which facilitated dispersal across deeper water regions within Laurentia. Timing of many dispersal events are correlated with major transgressions, such as during the Sandbian Age (Fig. 7) as larvae could disperse over physical barriers. In addition, several speciation events occur during times of rapid sea-level change, such as during the Darriwilian and late Katian–Hirnantian ages (Fig. 7). Furthermore, there is evidence that rapidly fluctuating sea-level influenced the alternation of dispersal and vicariance processes in some lineages, as basins were connected and later separated (e.g., *Plaesiomys subcircularis* evolution in the Hirnantian Age, Fig. 5). The combination of fluctuating sea-level and variation in tectonic flexure within Laurentia promoted alternating dispersal-vicariance speciation patterns, such as within *Glyptorthis* and *Flexicalymene* lineages during the Blountian tectophase (Fig. 5). Three of the four temporal bins include clades with alternating speciation histories, a pattern previously reported by Stigall et al. (2017) as resulting from cyclical connectivity of basins which alternatively promote and hinder speciation. Thus, the patterns recovered here further support Stigall et al.'s (2017) BIME model as a characterization of speciation and diversity accumulation processes.

Once the Taconian Orogeny began on the southern margin of Laurentia, increased vicariant speciation processes in both brachiopod and trilobite clades (Table 3) were promoted by the emplacement of barriers or rejuvenation of existing structural highs (Fig. 7). In particular, the brachiopod genus *Plaesiomys* and the trilobite genus *Flexicalymene* exhibited higher rates of vicariance speciation, possibly because both were largely endemic to Laurentia and speciation was driven mainly by tectonic events. The timing of vicariance events are broadly synchronous between brachiopods and trilobites (Fig. 7), indicating that although the clades had different larval tactics, environmental factors may have influenced these clades similarly. However, emplacement of barriers during the Taconian Orogeny seems to have affected benthic trilobite larvae more strongly than planktic brachiopod larvae, as trilobites exhibit the highest percent of vicariance speciation throughout this event (T2 and T3 time slices; Table 3). During the late Katian to Hirnantian (T4 time slice), brachiopods exhibited the highest amount of speciation via vicariance, which was largely due to the major regression that occurred during this time that may have led to subaerial exposure of land and topographic highs, which would have blocked dispersal. The elevated speciation that takes place during the late Katian and Hirnantian ages (T4 time slice) indicates that rapid fluctuations in climate and sea-level promote speciation processes in some clades, a time where other clades exhibited severe diversity decline during the end-Ordovician extinction (Fig. 7).

5. Conclusions

This study is the first of its kind to utilize Bayesian dating methods and maximum-likelihood biogeography for Paleozoic taxa. Time-scaled phylogenies and biogeographic histories were estimated for ten brachiopod and trilobite clades to compare speciation processes and dispersal routes through the Middle to Late Ordovician. Speciation types were dominated by dispersal, with varying percentages of vicariant speciation. Biogeographic evolution of most clades was optimized by models that incorporated long-distance founder-event speciation, indicating this was an important speciation process for Middle to Late Ordovician taxa. Dispersal was facilitated by volcanic island arcs and shallow-water carbonate basins acting as stepping-stones among paleobiogeographic areas and paleocontinents. On longer geologic timescales, most speciation events within clades took place during times of substantial climate change, notably global cooling. Several speciation events within brachiopod lineages during the Late Ordovician Hirnantian Age do not indicate depressed speciation associated with the Late Ordovician extinction pulses, indicating that fluctuating climate conditions promoted speciation in some Laurentian clades. During the Dapingian through late Sandbian ages, dispersal occurred among major paleocontinents and was facilitated by major ocean currents and gyre systems. Global cooling throughout the study interval could have led to a spin-up of ocean currents, thus greatly affecting the long-distance dispersal potential of larvae, especially during the GOBE. During the latest Sandbian to Katian ages speciation events were restricted to Laurentia, and were controlled by tectonics, upwelling zones, and

surface currents. Notably, paleoclimate and oceanographic factors impacted trilobite and brachiopod larvae similarly, as vicariance events occurred broadly synchronously between these clades. We found that larval type and time spent in a larval phase were the main factors that influenced the long-distance dispersal exhibited by trilobites and was the key determinant of dispersal patterns among focal taxa rather than larval position in the water column. To further elucidate the links between evolution and Earth system processes in the Ordovician, additional phylogenies from various clades are needed. This effort will support increasingly powerful statistical techniques utilizing probabilistic methods, and will elucidate other speciation patterns hidden in paleontological collections, ultimately leading to a deeper understanding of speciation type, patterns, and processes across major climate shifts and through time.

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